

(1) to be rendered quite sure that *R. cœnosus* is the plant that now inhabits those ditches, and (2) that it was the true *R. hederaceus* alone that grew there formerly. I have most frequently found *R. cœnosus* in rather elevated situations, where no source of artificial heat could affect it.

12. *R. hederaceus* (Linn.); leaves all roundish reniform with 3-5 shallow rounded lobes widening to their base, petals scarcely exceeding the calyx, style prolonging the inner edge of the ovary, carpels $\frac{1}{2}$ -oval or $\frac{1}{2}$ -obovate with a lateral point.

R. hederaceus, Linn. *Sp. Pl.* 781; *Eng. Bot.* t. 2003; *Reichenb. Icon. Fl. Germ.* iii. Ran. t. 2.

Stem floating or creeping upon mud, branched, nearly round. Leaves usually spotted; lobes separated by shallow notches, widening gradually from their base to a narrow rounded end, often broadly triangular, entire or rarely with a slight notch at the top. Petioles long, semicylindrical. Stipules long, much adnate, blunt, denticulate. Peduncles not narrowed upwards, much falling short of the leaves. Flowers very small. Petals about equalling or a little exceeding the calyx, narrow, 3-nerved. Stamens 6-8. Stigma short, oblong. Receptacle spherical, naked. Carpels compressed below, blunt and inflated above, inner edge nearly straight, laterally tipped with the style or pointless.

Flowering from June to September.

This plant is probably generally distributed, but as *R. cœnosus* is often mistaken for it, I may mention that I know of its existence at Inverarnan at the head of Loch Lomond, near Llanberis in Caernarvonshire, Lanwarne in Herefordshire, Needwood Forest in Staffordshire, Tiptree Heath in Essex, Triplow and other places in Cambridgeshire, near Haverfordwest in Pembrokeshire, Ninham in the Isle of Wight, and Bovey Heathfield in Devonshire.

XXXIV.—*On the Mechanism of Aquatic Respiration and on the Structure of the Organs of Breathing in Invertebrate Animals.*
By THOMAS WILLIAMS, M.D. Lond., F.L.S., Physician to the Swansea Infirmary.

[With a Plate.]

[Continued from p. 329.]

General and Minute Anatomy of Branchial Organs in the Gasteropod Mollusks.

THE author is not acquainted with any English or continental researches on the subject of the present paper. While the

organs and the process of breathing in the Lamellibranchiate classes have engaged the study of various able observers, no special attention has at any time been given to the minute and ultimate anatomy of these parts in the higher Mollusca. General views can only securely rest on correctly ascertained particulars. The laws which govern the structure and functions of individual organs of animals may be discovered with far greater certainty by tracing the advancing phases of their histological elements throughout the zoological series, than by following the mutations which occur in the progress of their embryonic development in one class. Comparative anatomy is still very deficient in such information. The general anatomy of organs has been ably written: their histological anatomy remains untold. The information to be drawn from the serial history of any given structural element of any given complex organ is more calculated to illustrate the homology of that organ and the architectural design under which it has been built, than any knowledge which can be attained by a descriptive account of its mere general conformation. The inmost constituent of structure may display greater invariableness of character than external outlines and the gross configuration. It is only by such a serial history that that which is essential to an organ can be eliminated from those superadded and accessory parts which are separable and non-essential. For instance, it is quite certain (see a memoir on the Serial Histology of the Liver (under the title of the Physiology of Cells) by the author, in Guy's Hospital Reports for 1848), that the same idea of the liver cannot be acquired by tracing the stages through which the organ passes in the embryo of the mammal, as that which is obtained by exhibiting consecutive pictures of the form under which it occurs in the successive links of the animal chain. There is much that is deceptive and fallacious in general resemblances and leading analogies. The ultimate and the particular must be seized before the comparison of general conditions can become correct and complete. How far-sought and really worthless it were to assert, that a single cell of the mammalian lung finds its counterpart, its prototype, in the membranous vesicle on the dermal surface of an *Asterias*, in which the process of respiration is carried on! In such an alleged analogy how many real deep differences are ignored! What a wide space is overleaped by simplicity and ignorance! How unsafe are generalities in science when unsupported by *ultimate* knowledge, by facts and details! On the other hand, how utterly valueless are figures, facts, and particulars, unless they form the substratum of *some* generality! To apply them to the maintenance of *any* theory invests them with life, renders them mutually coherent. Aban-

done to themselves they may be likened to grains of sand, between which there is no cohesion. These few preliminary remarks are made, at once, in apology and explanation of the plan of investigation which the author has adopted in these papers. He has sought at the expense of great labour, and heavy cost in several senses, to amass such a store of minute facts as will constitute at another time the ground of an appeal in support of a wide generalization. With this explanation he will now proceed to complete the serial history of the organs of respiration in Invertebrate animals.

In a former paper it was stated, in relation to the gills of the Lamellibranchiata, that from the Tunicata to the highest mollusk of this class, there prevailed a unity of structure which acknowledged no single real exception. In every form of branchia the blood-channels were straight, parallel, and non-communicating; that at the free border of the gill they returned upon themselves in form of loops, and that thus the afferent layers of vessels became separate and distinct from the efferent; that whether these layers were two or four in number, the real architecture of the organ remained unchanged*.

These fundamental facts will be found to pervade every variety of gill to be found among the higher class of the Gasteropod and Cephalopod Mollusca. In fact, wherever there is a separately developed branchia within the range of the Molluscan subkingdom, these principles of organic construction will receive an illustration. But between the Lamellibranchiate and Gasteropod gill, several important and striking differences exist. In the former the blood-channels are of large bore; they are capable of carrying a voluminous column of fluid: such a fact implies that in the organ of respiration in this class the fluids are not minutely multiplied and subdivided, and that consequently the contact between them and the external aërating medium is less intimate and complete. Another interesting fact to be noted is, that the corpuscles of the blood of the Lamellibranchiata are

* In the paper to which I refer, I promised to show that the apparently rectangularly-arranged blood-channels of the branchiæ of the Tunicata were not *real* exceptions to the rule stated. In the collected volume of these memoirs, it will be proved beyond doubt that the ultimate vessels in the pharyngeal gills of these inferior mollusks are disposed in "parallel, straight, non-communicating order," and that the crossing which takes place between the larger and the smaller blood-channels is a mere appearance depending upon the mode in which the gill is folded in the cavity. It will then also be shown that the ultimate blood-vessels in the branchiæ of the Tunicata are bounded by hyaline cartilages which also define the channels, precisely in the same manner as is done by the corresponding cartilages in the gills of the higher Lamellibranchs.

considerably larger * than those of the blood of the Gasteropod and Cephalopod mollusks. This difference flows naturally from the greater diameter which the blood-vessels of the former present as compared with those of the latter. On another occasion and in another place, the author will show that the same differences of size distinguish the blood-corpuscles of the lower Crustacea from those of the higher. This is either the consequence or the cause of the disparities of calibre in the branchial vessels which occur in these two sections of the same classes. They are visible facts which bear most explanatively upon not only the morphyic, but upon the subtler organic and chemical differences which mark the nutritive fluids of a less highly organized animal from those of another of higher standard; for it scarcely admits of doubt that the *vital standard*, the nutritive value of any given animal fluid, bears a direct ratio to the numerical amount of its floating corpuscles. As in the animal scale followed upwards, the floating globules of the blood become smaller and smaller and more and more numerous, correlatively the circulating channels gradually decrease in sectional area, become more and more subdivided and multiplied, until at length in the higher mammals the bore of the ultimate capillary exceeds little the diameter of the individual blood-corpuscle. These general views will serve to impart meaning to the minute anatomical details which are now to follow.

The *Tubulibranchiate* genera, *Vermetus*, *Dentalium*, and *Margilus*, are commonly placed at the bottom of the Gasteropod scale. For this disposition no reason can be drawn from the position and general anatomy of the branchial cavity or from the structure of the gills. M. Philippi† gives a figure which the author has copied (Pl. XI. fig. 1), in which the organs (*a* & *b*) contained in the respiratory chamber are clearly exhibited. The gills (*a*) are as perfectly pectinated, that is, they conform in figure and structure with those organs in the higher Gasteropods which are described as ‘pectinate’ gills‡. They occupy

* The measurements upon which this general statement is based will be published in the next paper on the Blood in the ‘British and Foreign Med.-Chir. Review.’

† *Enumeratio Molluscorum Siciliae*; and *Règne Animal*, pl. 62.

‡ The word ‘pectinate,’ as will be subsequently shown, is anything but descriptive of the real figure of the branchial laminæ of the Pectinibranchiata. To describe them as comb-like is to suggest a very false comparison. If the naturalist who first coined the word had isolated a *single* leaflet from the gill of a Pectinibranch and defined its *outline*, such a word never could have suggested itself. The same ridiculous disparity between the thing and the name will be found to occur in other designations of Orders. False titles like these—terms indeed constructed upon imperfect knowledge—illustrate the difficulty which must ever attend the attempt to

the same position in the branchial sac, that is, on the roof, and distant from the rectum (*b*). One border of the leaf is strengthened by a penknife-shaped cartilage, such as that which will be defined in the Pectinibranchiates. The breathing crypt in *Siliquaria anguina* is depicted by Philippi as having the same configuration. The branchiæ differ but triflingly from those of the former genus. By this observer, these parts are sufficiently clearly delineated in the two preceding Tubulibranchs to justify the inference that the branchiæ are formed precisely on the plan of those of the Pectinibranchiata. So similar to that of the latter order is the general cavity, so analogous the contained parts, so identical in structure the branchiæ, that it is difficult to conceive why *Vermetus* should be called a Tubulibranch, and *Buccinum* a Pectinibranch. In minute anatomy, the description which at another time will be given of the branchiæ of the latter will apply also to those of *Vermetus*. When species, whose vital organs are so similarly constructed, are placed at opposite extremes of an extended scale, the *anatomist* may well exclaim,—how artificial, partial, and arbitrary is the classification of the mere naturalist!

The Branchiæ of the Chitonidæ.

A *Chiton* has a carapace like an isopod Crustacean, a dorsal vessel like an Annelid, bilateral symmetrical reproductive viscera like an acephalous Mollusk, a head and foot like a patelloid Gasteropod, a posterior anus like the Fissurellidæ, and branchiæ like those of the brachyurous Crustacea! Such manifold affinities at once unite and sever this odd group from several most dissimilar classes. Measured by the standard of its branchial organs alone, it deserves a higher rank than that accorded to it by the side of the Patellidæ. The anatomical position of these organs nevertheless allies the *Chiton* to the *Patella*. In both, they are placed in the furrow between the border of the foot and the edge of the mantle. But in structure they are totally unlike. Imagination may indeed construct ideal analogies. If a branchial cone (fig. 2) were placed on either side of the anal debouchure in *Chiton* and then simply enlarged without change of figure, the branchiæ of *Fissurella* (fig. 10) would be simulated. They are organically different from those of *Emarginula* (fig. 9) and *Patella* (fig. 5). In structural characters the gills of the last two genera bear the same relation to each other

establish a true and natural terminological system in zoology before the real structure of animals is made known. The mere naturalist can never find himself in a position to construct a consistent "terminology." This task, so important to the progress of knowledge, must be jointly undertaken by the philosophic anatomist and the descriptive naturalist.

as that which subsists between those of *Chiton* and *Fissurella*. The ultimate respiratory laminae in the last two are bilateral, resting, that is, on either surface of a common axial plane. In *Emarginula* and *Patella* they rise from one surface only of a common basis. In *Patella* that basis is fixed, in *Emarginula* it is free. The branchial system of *Chiton* is distributed and subdivided, that of *Fissurella* is centralized in place and united in structure. In anatomical arrangement they are precisely the same. It should however be remembered, while discussing the generic affinities of the Chitonidæ, that, according to Cuvier's* dissections, the branchiæ in *Chiton spinulosus* (Linn.) are only one-sidedly laminated, resembling the arrangement of the teeth of a comb. By Forbes and Hanley† the branchiæ in the British families are defined as "forming a series of lamellæ between the mantle and the foot on each side." By Mr. Clark those of *Chiton fascicularis* are described as consisting of "a cordon between the mantle and the foot, composed of fifteen oblique cord-like, short, close-set, pale brown filaments on each side ‡." This description is calculated to mislead. The branchiæ in the Chitons are neither 'lamellæ' nor 'filaments.' They are complexly constructed organs (Pl. XI. figs. 2 & 3). Each 'filament' or 'lamella' (Forbes) is a separate and distinct fabric. Not less so than one of the cones of the gill in the Crab, or one of the penknife-shaped processes of the branchia of the Fish. In number these conules differ according to the species. A row of fifteen occurs in *Chiton fascicularis*, of seventeen in *C. cinereus*, of only ten in *C. asellus*, on each side of the body. They amount to eighteen in *Chiton discrepans*, to twelve only in *C. ruber*, to eighteen in *C. quinquevalvis* (Brown), and even to twenty-four on either side of the body in *C. marmoreus*. Several other species of Chitons are described in works on British Mollusca. In all, the branchiæ are overlooked. Numerous comparisons of the young with the old would be necessary to prove that in the adult state of each species these organules are constant characters. If they are, in descriptions of species a correct account of them, as regards number, size and position, should be included. They are well known to vary in size, apparent form, and in situation, relatively to the transverse median line of the body in different species, but in plan of formation or design they present no diversities. A branchia (figs. 2 & 3) in the genus *Chiton* may be typically described as a process of the mantle, consisting of a wedge-shaped axis (*b*), from whose opposite plane surfaces

* Mém. sur les Mollusques; and Règne Animal, pl. 68. vol. sur les Mollusques.

† British Mollusca, vol. ii. p. 391.

‡ British Marine Testaceous Mollusca, p. 249.

project at right angles secondary laminæ (*a, a, a*), laid flatwise the one upon the other from the base to the apex of the process. The laminæ (fig. 4 *d*; figs. 2 & 3 *a, a, a*) are largest at the root, smallest and tapering at the further free end. Each leaf (fig. 4 *d*) being attached only at one border, is capable of floating freely in the water. This is a point of immense functional advantage. The aërating current, however, is otherwise brought under muscular control. The row of gills, being disposed in an angular groove between two strongly contractile and extensile parts, namely the edges of the foot and mantle, are mechanically operated on by the current thus muscularly set in motion. Thus the laminæ are separated from one another.

The gills of *Chiton* are much more parenchymatous or fleshy than those of *Patella*. They possess an obvious power of collapsing and expanding. Muscular fibres are disposed variously throughout the entire gill. Even the borders of the leaflets are contractile (fig. 4 *d*). But the axial plane, in which the two large vessels (fig. 4 *a* & *b*) are lodged, is conspicuously fleshy and muscular. By the fibres situated in this axis the whole process may be shortened, and drawn strongly up towards the base. This power may be given in order to protect the part, or to quicken the circulation, or effectually to cleanse the gill of effete water. Each branchial process carries in its central plane two large vessels (*a, b*). They are connected with two main trunks which run along the edge of the mantle. They are respectively afferent and efferent. Thus far the apparatus is simple. The circulation in the laminæ is infinitely more complex (fig. 4). From the main afferent vessel (*a*, arrow) of the branchial process secondary branches (*e*) proceed. These latter run along the attached border or root of each leaflet. A similar secondary efferent vessel runs parallel to it on the other side of the same border (*e'*). The two vessels are connected together by means of the looped, parallel, ultimate blood-channels of the laminæ (*c, c'*). These latter are the true respiratory capillaries. They form in the substance of the leaflet *two layers* of vessels. The upper loops into the lower layer at the free border (*d*) of the lamina. Thus then the vital fluid flows, in horizontally parallel streamlets, of extreme minuteness, along the upper aspect of a sheet, itself flattened in the highest degree; following the direction of the loops, it curves round at the distal margin, returns in a similarly distributed stratum along the inferior face of the lamina, and reaches in the form of an arterial fluid the efferent vessel at the fixed base. Although these ultimate blood-channels are *unquestionably* separately walled conduits, they branch here and there and unite with those in the neighbourhood. This branching however so seldom occurs, that each vessel may really be

defined as maintaining its individuality from the beginning to the end of its course. This fact identifies the branchiæ of the Chitonidæ with the Molluscan type, and severs them from the Crustacean. This is an anatomical character of essential importance*.

Although an ultimate leaflet from the gill of the Chiton has precisely the same *figure* as the corresponding part of the gill of a brachyurous Crustacean, its real structure is demonstratively Molluscan. The microscope is thus enabled to prove, that beneath an exterior general resemblance there lies hidden an essential identity of organization. In the Chiton, as in *all mollusks*, the *branchial* vessels are individualized channels bounded by distinct walls. In the Crustacea the blood traverses wall-less lacunose passages, and forms invariably only a single stratum in its course. These facts are beyond question. They prove that the Chitonidæ are far more intimately allied to the Mollusk than to the Crustacean. They establish a new principle in homology. They prove that conformity in the last elements of structure signifies more than the superficial analogies of outward form.

Another striking point of dissimilitude between the gill of the Chiton and that of the Crab, is that in the former the *whole lamina*, but most conspicuously the borders, is covered by a comparatively dense *ciliated epithelium*. Cilia do not exist in the Crustacea. It is possible that these vibratile appendages may exist on the branchiæ of Gasteropod Mollusks, and not on those of Crustacea, because in the former the blood moving in the ultimate vessels can be exposed to the agency of the aërating element *only on one side*; whereas, as formerly explained, in almost

* I would here confess to the naturalist who may perchance repeat these observations, that no researches in which I have ever engaged have required so much *training of the eye*, and *familiarizing of the mind* with the appearances under study, as the ultimate characters of the vascular apparatus of the gills in the Cephaloporous Mollusca. Numerous difficulties occur. The same doubtful point must be tested in very different modes, in the recent and preserved specimens, and by aid of various chemical agents. In the Acephalous Mollusks, as in the Crustacea, the ultimate blood-channels become unquestionable at the first glance. Not so in the branchiferous Gasteropods. The vessels are smaller and covered with a denser epithelium; the tissue is contractile and softer, the parts of difficult access, &c.; but notwithstanding these difficulties, I believe that the real and true anatomy of these parts is faithfully given in the present memoir. It is the first occasion in comparative anatomy on which an attempt has been made to unravel the *ultimate character* of any part of the circulating system of the Mollusca. I am disposed to attach importance to what is true of the branchiæ in this sense, since it may hereafter prove of service in deciphering the last vessels of other tissues and organs. I would only in this place and at present venture to observe, that the *lacunar* theory of Milne-Edwards is incontestably in every sense more applicable to the Crustacea than to the Mollusca.

every Crustacean the extreme blood-passages are equally exposed on both sides of a single current to the action of the surrounding medium. Thus the area of exposure being the same, the functional value of a Crustacean gill may be equal to that of a Molluscan, albeit the circulatory system of the latter may be incomparably more perfect and elaborate than that of the former. A curious fact may here be mentioned, as connecting the branchial operations with the position of the cloaca: that in the Chitonidæ the effete current of water flowing in the respiratory groove between the edge of the mantle and that of the foot sets *backwards* towards the anus—in the Patellidæ it sets forwards, towards the common position of the mouth and anus.

To recapitulate: it may be stated that in figure the gill of the Chiton is the counterpart of that of the Crab; in the ultimate arrangement of its vessels it conforms with the type prevalent throughout the branchiferous Gasteropods; in its fleshiness, the denseness of its epithelium, and in the presence of minute follicles on its surface, it allies itself with the branchiæ of the Nudibranchs. Nothing is more easy than to *prove* the presence of epithelium over the entire surfaces of the laminae. The waving of the cilia is visible throughout the whole extent of the surface. The cilia which are situated on the free margins (fig. 4 *d*) are much larger,—supported by correspondingly larger cells than those distributed over the flat face. Opportunities will afterwards occur for considering the question, *why*, in the organs of branchial breathing, *ciliary* epithelium should almost always clothe even the *ultimate* vessels, and *why* they should be as constantly wanting on the corresponding parts of the pulmonary or air-breathing series.

Branchial System of the Patellidæ.

It is proposed here to take the branchiæ of the genus *Patella* as the type of those of the remaining genera of this order. But it will be shown that the Fissurellidæ, Emarginulidæ, and Halio-tidæ, &c., differ strikingly both in the special and in the general characters of the branchial system from the Patellidæ. Though there may exist *other* features which in the judgement of the malacologist may justify the marshalling of these several genera under one and the same order, estimated by the branchial apparatus, the Patellidæ ought unquestionably to stand apart and alone. The author is deeply persuaded that minute *ultimate* histological questions will *some day* in the history of science exercise a far more potent sway over the minds of classifiers than they have hitherto done. Unity and uniformity reign with greater constancy in the small than in the great productions of

nature. The cell or the fibre, which the wondrous microscope only can reveal to human ken, is no less fixed and invariable in its structure than the huge bone or the stupendous brain.

In the *Patella* the heart stands in the geometrical centre of the body. It is situated above and behind the head. It is not perforated by the intestines as it is in the Bivalves. It is an elongated sac dividing in front into two main pallial trunks. These latter distribute arterial blood throughout the mantle*. From the mantle and the viscera it returns into the branchiæ and thence into the heart, to be redistributed over the body. This apparatus can be detected with perfect clearness in the uninjected subject.

In *Patella* the branchiæ (fig. 5 *a, a*) form a *circle*, which is interrupted only by a small notch for the admission of water. That is, the lamellæ are neither deficient behind nor before. The "cordon" is continued over that portion of the margin of the mantle which is situated in advance of the head. Thus, in *Patella* the branchiæ neither arise from, nor are in any way attached to, the neck of the animal. They are developments of the mantle alone. This point is one of specific importance. It proves that the *figure* used by the late Prof. E. Forbes was unphilosophical, because unsupported by anatomy. He said that the branchiæ of *Patella* were really only those of *Fissurella* and *Haliotis*, *fixed* to the mantle and extended all round, instead of being *free* plumes as in the latter. But it is at once obvious, that not only the branchiæ themselves, but the anatomical relations of them are radically different in *Patella* and *Fissurella* and *Haliotis* for example. If, indeed, the latter genera have no better title to a rank in the Patellidan group than that which is furnished by the branchiæ, they should receive at once a summary sentence of exclusion.

The branchial organ of *Patella* consists of a *double* row of leaves (fig. 5 *a, e*) oblong in shape (fig. 8), standing vertically on, and at right angles with the plane of, the mantle (fig. 5 *c, c*). They constitute a special apparatus distinct from that papillose, ciliated fringe (*d*) with which the extreme edge of the mantle is ornamented. They extend over the entire circumference of the pallial border. They are not attached to any part of the body of the animal. The outermost row of leaflets (*a*) is a little larger

* So clear and water-like are the fluid contents of these vessels in a fresh specimen, while expanding itself in the struggle to get out of its shell, that they may most readily, but most erroneously, be mistaken for *aquiferous canals*. As on a future occasion I shall have a great deal to say on the ill-understood subject of the aquiferous system of Mollusks, at present I only desire to indicate a source of misconception which has led many an acute naturalist into error.

than the innermost (*e*). By a poetical stretch of fancy it might be said that, being composed of two sets of laminae, though situated on the same side of the same base, they may justly be likened to the oppositely-placed laminae of the plumose free gills of the other Patelloid orders. But such a comparison would be indeed far-sought.

The branchiae of the vulgar Limpet, to the careless looker-on on Nature's marvels, appear so contemptibly familiar, that to subject such objects to a grave and minute philosophical examination must prove a severe trial to his patience and common sense. Alas! how short is the range of human sight! Beneath the familiar exterior of these common objects there lies an undiscovered machinery of startling beauty and perfection! These little organs will serve to unite the branchial systems of the two great groups of Mollusks, the Acephalous and Encephalous. Through their aid it will prove practicable to establish a *unity of branchial type* coextensive with the entire Molluscan series. They will convince the zoologist that Nature never changes either the plan of her action, or the design of her architecture, by senseless and ludicrous transitions. Her incomparable, unequalled skill lies in adapting a single principle to the most varied ends.

Of the two rows of laminae in *Patella* as just stated, the inner is composed of smaller leaflets than the more external. The smaller and larger leaves occur alternately in the series. Both are precisely the same in minute structure. Expert manipulation is required in order to obtain a complete view of the gill-processes *in situ*. The whole ring of the mantle to which they are attached should be removed. Every portion of the loose edge and fringe should then be cut away, leaving only so much as will hold the laminae in position. A small segment of this circle should be then placed in the cell of an object-glass, floated with water and covered with a slip of thin glass. The position of the laminae may now be changed at will, by slackening or extending the portion beyond the edge of the glass.

It will now be remarked, that each lamina (fig. 8) is a separate and distinct process, resting on, or proceeding from, a distinct base; that it is *not* a simple vertical sheet like the leaf of a book, of equal thickness at every part, at the edge and at the base; that it is not, what seemed certain to the naked eye, a compactly-structured *single* sheet. A far more intricate arrangement discovers itself. First, each lamina, as it stands in its place and *unstretched*, forms a concavo-convex outline (fig. 8). It bulges out (*a*) like a sail in the wind on one side; it is hollow on the other (*b*). This figure is due to the fact that the free border (*c*) is denser and less extensible than the intermediate membranous portion. Many advantages are secured by such an

arrangement. The individual laminae of the series mutually support one another by a more exact and rapid adaptation of the *vis-à-vis* surfaces. They are less liable to fold and wrinkle by the rapidly varying degrees of distension to which they are exposed by the action of the margin-muscles of the mantle. But the free border of each leaflet is further so constructed as to realize a great degree of elasticity (figs. 7, 6). On looking sideways, that is, directly down upon the edge of the leaflet, the eye discovers with perfect clearness an arched or vaulted outline (fig. 7 *c*; fig. 6 *e*) formed by the *curving* round of the blood-channels of one half or layer of the sheet, in order to run into those of the other half (fig. 7 *a, e, b*). It is by this method of viewing the object that the anatomist may convince himself that each gill-plate is really composed of two distinct and separated layers (figs. 6 & 7 *a, b-a, b*), united only at the margin (*c, c*), in exact accordance with the pattern of the *single* gills of the Lamellibranchiate Acephala.

The satisfactory determination of this point of structure is of great importance in this inquiry. It possesses all the power of a key as regards the after-stages of the investigation. So extraordinary is the uniformity of the *plan* on which the respiratory organs of the branchiferous Gasteropods are formed, that it may be inferred with perfect certainty that what is clearly proved to be true of one grade in the series will apply with essential accuracy to all the others. Extremely difficult therefore though it may be to unravel the minute structure of the gill-laminae of *Patella*, from the key-like power of the information thus only to be acquired, it is worthy of all the patience which the student can command.

Two facts of structure are then determined:—1st. That the plate is composed of two layers; 2nd. That those two layers are united by a looped arrangement at the margin. Now it may be proved with exact certainty, that each layer is composed of straight or wavingly parallel channels (figs. 6 *a, b*, and 7 *a, b*) laid on the same horizontal plane (fig. 6 *a*, as far as *i*), such that a *membrane* is formed. Although these channels are far less individually distinct than those of the gills of the Lamellibranchs, they are unquestionably blood-vessels, united together into a membrane-like series by delicate intervening fibres or membrane. Various kinds of proofs might be adduced in support of this interpretation.

The cilia follow the outline of each vessel (fig. 7 *a, b*) in a line-like manner. The vessels present a linear bulge like a tube. They can be seen to be filled with rows of corpuscles, clearly distinguishable from the fixed cells and epithelia which form the solid substance of their walls. Traced carefully in the direction

of the distal margin, they become more and more separated from one another (fig. 6 *d*). The interposed substance becomes more and more pellucid, until at length at the margin the vascular loops (*c, c*) stand out in unmistakeable eminence. So microscopic is the mechanism however, that it is impossible by *direct* view to state whether these vessels are separated by a water-fissure, such as that which exists in the gills of the Lamellibranchs, or whether they are joined by an intervascular membrane. In the former case, water would penetrate into the space (fig. 7 *e*) between the two constituent layers of the lamina; in the latter this space would be entirely closed from the external element. On a superficial view this point may appear very insignificant. On a deeper insight it becomes pregnant with functional and homological meaning. If the water could find a ready entrance into the interlaminar space (fig. 6 *e, g*), the column of blood flowing in each afferent and efferent blood-vessel (*a, b*), that is, in the trunks bounding that space, would be aerated on both sides, and the respiratory value of the organ would at once be doubled. It is almost certain that it does not and cannot. If the external water cannot and does not penetrate into this interlaminar space, then it must be filled by the vital fluid of the animal; for the space exists beyond doubt. If this latter supposition be true, it is quite certain that this fluid must be distinct from that which circulates in the laminar or proper branchial vessels. This doubt must for the present be left undetermined. Whether it be soluble or not, enough of the essential structure of the gasteropodan gill has been demonstrated to establish between it and the branchiæ of the Lamellibranchs an extraordinary resemblance; not a mere outline-similarity, but a closeness, almost amounting to an *identity* of constructive plan. If everything else in the patelloid organism exhibited the same degree of similitude to the system of the Lamellibranch as that which obtains in the branchial apparatus, the naturalist would not hesitate to define the Patella at once as the highest Acephalan and the lowest Encephalan. It must however be admitted, that the judgement of the classifier should not be swayed exclusively by special affinities. The question now arises, if these minute branchial leaflets of *Patella* really consist each of two layers, how are these layers tied together? They are fixed to one another by an intermediate system of threads (*trabeculae*) crossing each other in such a manner as to afford the most effectual mutual support (fig. 6 *h*; fig. 7 *g*). The points (fig. 6 *f*; fig. 7 *d*) to which these connecting fibres or bands (fig. 7 *f*; fig. 6 *h*) are attached to the vessels are swelled into nodules (fig. 7 *d*), which present a singular resemblance to the fleshy nodules on the branchial bars of the Mussel. Of course

they are much less visible than they are in the latter case, but in anatomical characters and relations they are in both cases most remarkably analogous. Now the interval between the two layers which is crossed by the threads just described, is indubitably filled with *some* fluid. What that fluid is, it is impossible at present to say.

The water-currents excited by cilia on the flat surfaces of the branchial laminae set, from the fixed, in the direction of the free border. The cilia which are distributed over the flat faces of the leaflets are very much smaller than those which fringe the margins. The exact position to which the former are attached in relation to the lines of the blood-channels cannot therefore be clearly defined. This, however, is an unimportant point, since the *aggregate* action of the cilia, as indicated by the setting of the current, may be easily proved.

The epithelium which lines the flat surfaces of the laminae forms undoubtedly a *continuous membrane*. It is consequently impossible that there can take place any water-currents between the individual blood-channels, such as those which figure so prominently in the mechanism of the Lamellibranchiate gills. The water-passages being wanting, it results that, in *this* Gasteropod, the branchia *is not penetrated by the aërating medium*. This fact should be regarded rather as a criterion of superior than of inferior organization. It signifies an increasing subdivision of the blood-streams. The blood-vessels being smaller, and the parietes being less dense and cartilaginous, exposure to the oxygenating medium *on one side only* suffices for the purposes of respiration. It is important in this place to remark, that if the *interlaminar* space of the branchial leaves of *Patella* could be *proved* to be filled with water and not with blood, *some* ground would be afforded, as will again be shown, for supposing that in these Mollusca the *external* water is actually admitted into the *penetralia* of the organism, forming an *aquiferous system*, and that it circulates like a nutritive fluid throughout the entire body. This, however, is a *fancy* as yet at all events totally unsupported by fact.

It is difficult to leave this part of the present inquiry without once more drawing attention to the homologous significance of the branchiæ of *Patella*. They are composed of two layers of vessels, opposed face to face, and joined at the margin. They are invested by a ciliated epithelium which is restricted to the *exterior* aspect of the organ. The constituent layers are separated by an intermediate space. In these several items of mechanism these branchiæ approximate most wonderfully closely to the type which is normal to the Acephala. If there be no meaning in this approximation, there can be no *unity* in the organic system of

nature, and the philosophic anatomist may indeed well abandon his studies in despair. In conclusion it should be remembered, that between a single leaflet of the gill of *Patella* and a single lamina of the same form and figure, taken from any small brachyurous Crustacean; the extremest difference exists. The Crustacean gill is far less perfect, more rude in every sense, as a purposive machinery. Carrying a single stream of blood, whose corpuscles are considerably larger than those of *Patella*, and which runs in irregular passages lying between two sheets of epithelium tied together only by means of accidentally distributed islets of fleshy tissue, it contrasts strikingly with the double-vessel system with the contractile and highly ciliated elements of which the Patellan gill is woven.

For reasons derived from other sources than those of the branchiæ, the genera *Emarginula*, *Fissurella* and *Haliotis* are placed by malacologists in the Patelloid group. The branchiæ of *Emarginula* (fig. 9 a, a) approach much nearer than those of *Fissurella* (fig. 10 a, a) to the type of these organs as they exist in *Patella*. The gills of *Emarginula* are attached to the base of the cervical cavity (fig. 9 d) on either side of the outlet of the intestine. They project forwards in form of tapering processes (a, a) on either side of the head of the animal. They are chiefly fixed at the base, but a slender membranous *frenum*, proceeding from the median line of each, connects them to that portion of the mantle which covers the roof of the cavity of the shell in which the head and rectum are situated. They are thus held in one position. They possess notwithstanding a slight power of expanding and collapsing. They are foliated only on one side (a, a) of a base. They are more comb-like than plume-like. In this particular of configuration they approach closely to the branchiæ of *Patella*. If the latter were seated on a free instead of a fixed base, the resemblance would be very near. Occupying a position on either side of the notch (b) in the shell, the latter should be regarded as playing as important a part in providing a fresh current of water for the branchiæ, as in conveying away the excreta.

The ciliary movements observable in this region both in *Emarginula* and *Fissurella* point to the same inference. Examined separately under the microscope, a single leaf taken from the gill of *Emarginula reticulata* presents an outline not unlike that of *Patella*. It is, however, more lancet-shaped. In ultimate minute structure it corresponds exactly with the aptellidan model already figured. Its vessels run in parallel columns, looping at the free margin and covered by a ciliated epithelium. The interlaminae space, so unquestionable in the gill-leaf of *Patella* (fig. 6 e); is here however much more contracted

and less distinguishable. In other words, the layers are so intimately soldered together as almost to obliterate the intervening space. The layers nevertheless carry separate and distinct planes of blood-channels. In *Fissurella* the organs of breathing (fig. 10 *a, a*) consist of two plumose tapering processes (*a, a*), projecting forwards (when fully expanded) to a considerable distance under the anterior vault of the shell. They are capable, like the arms of a Brachiopod, of being coiled up on themselves. They are distinguished from those of *Emarginula* in having a double system of leaves. These gills therefore present rather a pinnate than a pectinate figure. They stand at the sides of the chamber, the roof of which is perforated by the opening at the apex of the shell. This orifice admits fresh water into this space; it also conveys externally all refuse excretions. In the disposition of the vessels, in the character of the ciliary epithelium, in the fact of two planes of vessels, the branchiæ of *Fissurella* conform to the standard of the Patellan gill.

The branchial plume of *Acmaea testudinalis* extends to a great distance beyond the limits of the shell. It is fixed to the neck of the animal at the root of the right tentacle. It is bisymmetrically foliated; each lamina in its ultimate anatomy follows the Patelloid type. The gills of *Propilidium ancyloide* consist of two small feathery processes attached to the dorsal surface of the neck of the animal. They incline in a parallel direction to the right side of the cloacal cavity. They are free processes, and furnished with a double series of leaves, supported by an axial base, in which the afferent and efferent branchial vessels are lodged.

In *Puncturella noachina* the gill is non-symmetrical. It occupies a special and spacious chamber on the left side of the neck and foot. It is a pinnate structure highly ciliated, the lamina being large.

Judged by the structure and relations of the branchial system exclusively, the Fissurellidæ are undoubtedly placed in their true serial position by Forbes and Hanley, namely intermedially between the Limpets and Haliotidæ. They are Scutibranchiate. This cannot be said of *Acmaea* and *Propilidium*. The branchia here is not shielded by a fold of the mantle. Nor are they Cyclobranchiate, for the branchial processes are free plumes. If affinity is to be decided by structure rather than position, both *Acmaea* and *Propilidium* should be classed with the Scutibranchs.

The branchiæ in *Haliotis* (fig. 11) are sufficiently large to enable us to trace satisfactorily the distribution of the larger blood-channels. They will suffice to illustrate the circulatory apparatus of the gills in all the other Scutibranchs. The author's account is drawn from an examination of a specimen

preserved in spirit, aided by the successful injections of Milne-Edwards.* *Haliotis tuberculata* is a typical Scutibranch. The branchiæ (fig. 11 *a, a*) are lodged in a spacious enclosure of the mantle on the left side of the body. They are attached at the base by means of the vascular trunks; on the inferior surface to some extent of their length, by means of a membranous *frenum*. They are doubly laminose; that is, between two parallel trunks (*b, b* & *c, c*), a vein and an artery, which run from the base to the apex of each gill, there lie transversely two series of leaves (*a, a'*, *a, a'*) which are traversed by the blood of the afferent vessel (*b*) on its path to the efferent vessel (*c*). Here again, as in all the Gasteropod Mollusks, the gills are observed to conform in *general* structure to those leafy piles which fill the thoracic cavity of the Crab; but how totally different in the minute parts of their organization! In *Haliotis* the heart (*e*) is *systemic*. The blood, freshly arterialized, returns directly from the branchiæ into the auricles (*d, d*); from the ventricle (*e*) it is driven into the systemic aorta (*f*). At the roots of the branchiæ the venous blood converges into capacious, but not lacunose, afferent trunks (*b, b*), along which it is conducted to the branchial laminæ. The vascular system of the laminæ (fig. 12) is the same in every respect as that already described and figured in *Chiton* and *Patella*.

Each lamina carries two layers of horizontally stratified, uniformly diametered tubes, united to one another laterally, and to those of the opposite venous stratum by transverse threads. Each leaflet consequently consists of two layers or planes of blood-channels, joined together at the free margin, and covered on their external surfaces by a ciliated epithelium. A thin film of water moves wavily from the fixed to the free borders: it is sustained in motion by the vibration of the cilia. Such an arrangement proves that not only the blood to be aërated, but the water which aërates, is required in the act of respiration to be divided to the utmost degree. As far as this inquiry has proceeded, it must have been observed, that although the plumose or pinnate form of gill is constantly adopted as the most convenient figure in accordance with which to construct the respiratory organs both in Mollusca and Crustacea, the resemblance never proceeds beyond the exterior conformation and the disposition of the larger vessels. Beyond and deeper than this limit the microscope establishes an irreconcilable difference between the Crustacean and Molluscan gill. It exemplifies the supreme value of this instrument in zoological research. But apart from these physical considerations, a chemical ground of dissimilarity be-

* *Annales des Sciences Naturelles*, tom. viii. 1847.

